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# Conditional persistence in logistic models via nonlinear diffusion

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A nonlinear diffusion process modelling aggregative dispersal is combined with local (in space) population dynamics given by a logistic equation and the resulting growth-dispersal model is analysed. The nonlinear diffusion process models aggregation via a diffusion coefficient, which is decreasing with respect to the population density at low densities. This mechanism is similar to area-restricted search, but it is applied to conspecifics rather than prey. The analysis shows that in some cases the models predict a threshold effect similar to an Allee effect. That is, for some parameter ranges, the models predict a form of conditional persistence where small populations go extinct but large populations persist. This is somewhat surprising because logistic equations without diffusion or with non-aggregative diffusion predict either unconditional persistence or unconditional extinction. Furthermore, in the aggregative models, the minimum patch size needed to sustain an existing population at moderate to high densities may be smaller than the minimum patch size needed for invasibility by a small population. The tradeoff is that if a population is inhabiting a large patch whose size is reduced below the size needed to sustain any population, then the population on the patch can be expected to experience a sudden crash rather than a steady decline.

## 1. Introduction

### 1.1. General introduction

Various types of organisms form aggregations (swarms, flocks, herds, etc.) for various reasons. There has been a considerable amount of work on modelling the process of aggregation and studying its effects on interactions between species. In this article we consider the effects of intraspecific aggregation on the population dynamics of a single species. We model aggregation with a density-dependent diffusion process where the rate at which individuals move is decreased by the presence of conspecifics, at least at low densities. That mechanism is similar to area-restricted search, except that individuals are envisioned to be searching for conspecifics rather than prey or other resources. Such mechanisms may be deduced from empirical considerations. For example, Turchin [21] gives an example in one space dimension appropriate for insects that use visual cues to orient upon conspecifics. We then couple the aggregative dispersal mechanism with local population dynamics described by a simple logistic equation and analyse the dynamics of the resulting model. Because the model is order preserving, it turns out that its dynamics are largely determined by its equilibria, so most of our analytic efforts are devoted to

studying those equilibria and their stability properties. We conclude that aggregative dispersal can have qualitative effects on population dynamics, which cannot be induced by passive diffusion or by diffusive dispersal with mutual avoidance. In particular, even though the local population dynamics at any spatial location are assumed to be logistic, the global dynamics of aggregative models may display an Allee effect. In other words, although the local population dynamics would predict either extinction or unconditional persistence for a population restricted to a single location, the full model sometimes predicts conditional persistence, where any sufficiently large population will persist but where small populations will go extinct.

A good general discussion of modelling animal aggregation is given by Grünbaum and Okubo [9]. Some discussion of the reasons why aggregation might be adaptive is given in [2, 19]. There has been much theoretical work on the effects of aggregation on competitive or host–parisitoid interactions (see [20] and [10], respectively, and the references therein). The formulation of continuum models for aggregation is described in [9], and treated in some detail in [7, 8]. An example of a model involving area restricted search is carefully constructed in [13]. Alternatively, a spatially discrete model is derived in [14].

In [3], we studied logistic equations with density-dependent diffusion and found that if the diffusion rate increased with density, the predictions of the models were qualitatively the same as those for logistic equations with passive diffusion. Specifically, we considered a population inhabiting a bounded region with a hostile exterior and found that the models either predicted persistence for any population (if the region was large, the diffusion rate was small, and/or the local growth rate was large) or extinction for any population (if the region was small, the diffusion rate was large, or the local growth rate was small). However, as we shall show in the present article, if the diffusion rate decreases with density at low densities, then the models predict conditional persistence in some cases. In other words, they may predict persistence for large initial populations but extinction for small.

In the remainder of this section we describe the models and state some background results. In the next section we perform the mathematical analysis of the models. That section is somewhat technical. In the last section we give a discussion of the implications of our general results in the context of a specific model. We conclude with a non-mathematical discussion of the implications of the results.

### 1.2. Models and results of previous analysis

The models we consider describe scenarios in which a population inhabits a bounded region $\Omega$ with lethal exterior, grows logistically within the region, and disperses through the region via a diffusion process (i.e. by random walks) in which the rate of dispersal depends on the population density. We shall write the logistic part of the model as

$$\frac{\mathrm{d}u}{\mathrm{d}t} = m(x)u - cu^2, \tag{1.1}$$

where $u$ represents the population density, $m(x)$ is a spatially varying local growth rate, and $c$ measures the strength of logistic self-limitation. The diffusive part of the model will be written as

$$\frac{\partial u}{\partial t} = \nabla \cdot d(x, u)\nabla u, \tag{1.2}$$

where again $u$ represents population density. In (1.2), the coefficient $d(x,u)$ represents the diffusion rate. Recall that this coefficient is proportional to the mean-square distance that an individual moves in unit time (see [16]). We shall assume that the diffusion rate remains strictly positive but at low densities decreases with population density. This assumption reflects a tendency for the population to aggregate, because individuals slow their rate of random movement in the presence of conspecifics if the density of conspecifics is not too high. The mechanism is similar to the use of area restricted search by predators, which has been shown to induce aggregation by predators at locations with high prey density [13]. The difference is that instead of responding to prey density, individuals are assumed to respond to the density of conspecifics [21]. We can assemble our model from the terms in (1.1) and (1.2) to obtain

$$\left.\begin{aligned} \frac{\partial u}{\partial t} &= \nabla \cdot d(x,u)\nabla u + \lambda[m(x)u - cu^2] && \text{in } \Omega \times (0,\infty), \\ u &= 0 && \text{on } \partial\Omega \times (0,\infty), \end{aligned}\right\} \tag{1.3}$$

where the condition on $\partial\Omega$ corresponds to the assumption that the exterior of $\Omega$ is lethal. If we start with $\lambda = 1$ in (1.3) and rescale by $\tau = t/\gamma^2$, $\xi = x/\gamma$, then we obtain an equation equivalent to

$$\frac{\partial u}{\partial \tau} = \nabla \cdot d(\gamma\xi, u)\nabla u + \gamma^2[m(\gamma\xi)u - cu^2]. \tag{1.4}$$

Thus, if $d$ and $m$ do not depend on $x$, we can interpret $\lambda$ as arising from expanding or contracting the spatial region $\Omega$ by a factor $\gamma$ and then rescaling time appropriately. (Large $\lambda$ would correspond to a large region, small $\lambda$ to a small region. For $d$ and $m$ independent of $x$, rescaling the size of the domain $\Omega$ is mathematically equivalent to rescaling the diffusion coefficient while leaving the size of $\Omega$ fixed.) In general, $\lambda$ measures the ratio of the respective rates of population growth and dispersal throughout $\Omega$, with large $\lambda$ corresponding to a high growth rate relative to movement rate.

Throughout this paper we shall assume that the coefficients of (1.3) are smooth enough that the classical theory of parabolic partial differential equations and the elliptic equations describing their equilibria can be applied. That will typically require that $m(x)$ is Hölder continuous and that $d(x,u)$ and its first derivatives are Hölder continuous. An important feature of (1.3) is that it is order preserving, that is, if $u_1$ and $u_2$ are solutions with $u_1(x,0) \geqslant u_2(x,0)$, then $u_1(x,t) \geqslant u_2(x,t)$ with strict inequality for $x \in \Omega$ unless $u_1(x,0) = u_2(x,0)$. It follows (among other things) that almost all trajectories of (1.3) have $\omega$-limit sets that are subsets of the set of equilibria of (1.3) (see [3, 12]). Hence it is sensible to study the behaviour of (1.3) in terms of its equilibria. It turns out that to describe the set of equilibria of (1.3), we must introduce a related eigenvalue problem obtained by linearizing (1.3) about $u = 0$, namely

$$\left.\begin{aligned} -\nabla \cdot d(x,0)\nabla\phi &= \lambda m(x)\phi && \text{in } \Omega, \\ \phi &= 0 && \text{on } \partial\Omega. \end{aligned}\right\} \tag{1.5}$$

We have the following lemma [11, 15] (see also [3]).

LEMMA 1.1. *If $m(x) > 0$ on an open subset of $\Omega$, then (1.5) admits a unique positive principal eigenvalue $\lambda_1^+(d(x,0),m)$, which is characterized by having an eigenfunction $\phi(x) > 0$ on $\Omega$. All other positive eigenvalues of (1.5) are larger than $\lambda_1^+(d(x,0),m)$.*

In [3], we obtained results equivalent to the following.

THEOREM 1.2. *Assume that $m(x) > 0$ on an open subset of $\Omega$ and that $d(x,u) \geqslant d_0 > 0$ for some constant $d_0$. If $d(x,u)$ is non-decreasing in $u$, then*

(i) *if $\lambda \leqslant \lambda_1^+(d(x,0),m)$, then all positive solutions to (1.3) approach zero as $t \to \infty$;*

(ii) *if $\lambda > \lambda_1^+(d(x,0),m)$, then (1.3) has a unique positive equilibrium $u^*$ that is globally attracting among positive solutions.*

We also observed in [3] that in a simple example where $d(x,u)$ is decreasing in $u$, the above theorem is no longer valid. The present article was in part prompted by the example. However, we only assume here that the diffusion rate decreases with population density when the population density is low. Our model allows for the diffusion rate to increase in response to overcrowding.

Before we proceed to the analysis of (1.3) in this case, one more result is worth mentioning. The stability of the equilibrium $u \equiv 0$ in (1.3) is determined by the sign of the principal eigenvalue $\sigma_1$ of

$$\left.\begin{aligned} \nabla \cdot d(x,0)\nabla\psi + \lambda m(x)\psi &= \sigma\psi \qquad \text{in } \Omega, \\ \psi &= 0 \qquad \text{on } \partial\Omega. \end{aligned}\right\} \tag{1.6}$$

(The principal eigenvalue of (1.6) is the largest eigenvalue of (1.6) and is characterized by having an eigenfunction $\psi > 0$ on $\Omega$.) If $\sigma_1 < 0$ in (1.6), then $u \equiv 0$ is locally stable; if $\sigma_1 > 0$, then $u \equiv 0$ is unstable.

LEMMA 1.3. *Suppose that $m(x) > 0$ on an open subset of $\Omega$. If $\lambda > \lambda_1^+(d(x,0),m)$, then $\sigma_1 > 0$ in (1.6). If $\lambda < \lambda_1^+(d(x,0),m)$, then $\sigma_1 < 0$.*

DISCUSSION. This follows from the remarks in [3, p. 1049].

## 2. Analysis of equilibria

In this section, we establish the mathematical background needed to justify the conclusions we draw concerning the ecological implications of the model (1.3). To do so, as noted in § 1, we may focus our attention on the non-negative equilibria of (1.3). To this end, we find it useful to regard the $d(x,u)$, $m(x)$ and $c$ parameters in (1.3) as fixed (though subject to additional appropriate hypotheses) and analyse the resulting parameter-equilibrium pairs $(\lambda, u)$ as a subset of the Cartesian product $\mathbb{R} \times X$, where $X$ is a suitable space of functions. If we assume that $d$ is continuously differentiable in $x$ and $u$ with Hölder continuous partial derivatives of exponent $\alpha$, and that $m$ is Hölder continuous in $x$ of exponent $\alpha$, we may take $X = C_0^{2+\alpha}(\bar{\Omega})$, the space of twice continuously differentiable functions on $\bar{\Omega}$ that vanish on $\partial\Omega$ and

whose second partial derivatives are Hölder continuous of exponent $\alpha$. We may then regard the parameter-equilibrium pairs $(\lambda, u)$ as solutions to the operator equation

$$F(\lambda, u) = 0, \tag{2.1}$$

where $F : \mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega}) \to C^{\alpha}(\bar{\Omega})$ is given by

$$F(\lambda, u) = \nabla \cdot (d(x, u)\nabla u) + \lambda[m(x)u - cu^2]. \tag{2.2}$$

The analysis needed to describe the set

$$\{(\lambda, u) \in \mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega}) : F(\lambda, u) = 0 \text{ and } u \geqslant 0 \text{ on } \bar{\Omega}\}$$

divides into three parts. First, we use global bifurcation theory to establish that a continuum $\mathcal{C}$ of pairs $(\lambda, u)$ with $u > 0$ on $\Omega$ emanates from the 'trivial' solutions $(\lambda, 0)$ at the point $(\lambda_1^+(d(x, 0), m), 0)$. We then make a local analysis of $\mathcal{C}$ near the point $(\lambda_1^+(d(x, 0), m), 0)$ to show that initially $\mathcal{C}$ 'bends to the left' in the parameter space $\lambda$, so that there are pairs $(\lambda, u)$ with $\lambda < \lambda_1^+(d(x, 0), m)$ and $u > 0$ in $\Omega$. Finally, we determine the linearized stability of the equilibrium $u$ of (1.3) for all $(\lambda, u)$ in a neighbourhood of $(\lambda_1^+(d(x, 0), m), 0)$, augmenting the result of lemma 1.3.

It is clear from a comparison with theorem 1.2 that some additional hypotheses are necessary if the preceding description of

$$\{(\lambda, u) \in \mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega}) : F(\lambda, u) = 0 \text{ and } u \geqslant 0 \text{ on } \bar{\Omega}\}$$

is to hold. To this end, for the remainder of this section, we shall assume the following.

ASSUMPTIONS 2.1.

(i) $d(x, u)$ is $C^{1+\alpha}$ in $x$ and $C^3$ in $u$ for $(x, u) \in \bar{\Omega} \times \mathbb{R}$;

(ii) $m(x)$ is $C^{\alpha}$ for $x \in \bar{\Omega}$;

(iii) $c$ is a positive constant;

(iv) $d(x, u) \geqslant d_0 > 0$ for $(x, u) \in \bar{\Omega} \times \mathbb{R}$;

(v) $d_u(x, 0) < 0$ for $x \in \bar{\Omega}$;

(vi) $m(x_0) > 0$ for some $x_0 \in \Omega$.

Key among the above assumptions are (iv) and (v). In the aforementioned article of Turchin [21],

$$d(u) = \tfrac{1}{2}\mu - 2k_0 u + \frac{2k_0}{\omega}u^2,$$

where $\mu$, $k_0$ and $\omega$ are positive constants. It is immediate that $d'(0) = -2k_0$, so that assumption (v) is met. Moreover, $d(u)$ is quadratic in $u$ with positive leading coefficient $2k_0/\omega$. Since the discriminant for $d(u)$ is $4k_0(k_0 - \mu/\omega)$, assumption (iv) will be met, provided that $\mu/\omega > k_0$. Note also that we have strengthened the regularity hypothesis on $d$ to have $d$ thrice continuously differentiable in $u$, so that we can apply the results in [3] *verbatim* at a crucial point in our analysis. We acknowledge

that results comparable to those we establish in this section can be derived under less restrictive regularity assumptions on $d$ and $m$. However, our assumptions are certainly reasonable. Moreover, they allow for a mathematical presentation that is as accessible as possible, which we believe well deserves a biomathematical audience.

The 'global structure' of the set as a subset of $\mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega})$ follows from [3] (see also [18]), and we may gather the pertinent results in the following.

THEOREM 2.2. *Assume that assumptions 2.1 hold. Then the closure of the set*

$$\{(\lambda, u) \in \mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega}) : F(\lambda, u) = 0 \text{ and } u(x) > 0 \text{ in } \Omega\}$$

*contains a connected and locally compact subset $\mathcal{C}$ with the following properties:*

(i) $(\lambda, 0) \in \mathcal{C}$ *only when* $\lambda = \lambda_1^+(d(x,0), m)$;

(ii) *if* $\underline{\lambda} = \inf\{\lambda \in \mathbb{R} : \exists u \in C_0^{2+\alpha}(\bar{\Omega})$ *such that* $(\lambda, u) \in \mathcal{C}\}$, *then* $\underline{\lambda} > 0$;

(iii) *for all* $\lambda > \underline{\lambda}$, *there exists* $u \in C_0^{2+\alpha}(\Omega)$ *with* $u > 0$ *in* $\Omega$ *so that* $(\lambda, u) \in \mathcal{C}$.

REMARK 2.3. $\mathcal{C}$ is referred to as a continuum in the bifurcation theory literature. $\mathcal{C}$ is unbounded as a subset of $\mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega})$, by virtue of the fact that there is $(\lambda, u) \in \mathcal{C}$ for all $\lambda > \underline{\lambda}$. However, the maximum principle [17] guarantees that for any $(\lambda, u) \in \mathcal{C}$,

$$u(x) \leqslant \frac{\max_{x \in \bar{\Omega}} m(x)}{c},$$

so that there is a uniform upper bound on the equilibrium components along $\mathcal{C}$.

REMARK 2.4. There can be no arbitrarily small positive equilibria to (1.3) except for $\lambda$ near the critical value $\lambda_1^+(d(x,0), m)$.

REMARK 2.5. If assumption 2.1 (v) is replaced by the condition that $d(x,u)$ is non-decreasing in $u$, then theorem 1.2 holds. In this case, $\underline{\lambda} = \lambda_1^+(d(x,0), m)$ and for each $\lambda > \underline{\lambda}$, there is a unique positive $u \in C_0^{2+\alpha}(\bar{\Omega})$ such that $(\lambda, u) \in \mathcal{C}$. In this situation, $\mathcal{C}$ can be regarded as the graph of a smooth mapping from $[\underline{\lambda}, \infty) = [\lambda_1(d(x,0), m), \infty)$ into the function space $C_0^{2+\alpha}(\bar{\Omega})$ which takes the zero function as its value at $\underline{\lambda}$. Moreover, for each $\lambda > \lambda_1^+(d(x,0), m)$, the corresponding $u$ is the global attractor for non-negative non-trivial solutions to (1.3).

REMARK 2.6. As noted in § 1, theorem 1.2 is no longer valid if assumptions 2.1 are imposed and it may indeed be the case that $\underline{\lambda} < \lambda_1^+(d(x,0), m)$. In such a situation, problem (1.3) admits positive equilibria for $\lambda$ below the critical threshold $\lambda_1^+(d(x,0), m)$.

The next portion of our analysis of the positive equilibria of (1.3) seeks to identify conditions on $d(x,u), m(x)$ and $c$ that will guarantee the existence of positive equilibria for (1.3) for $\lambda < \lambda_1^+(d(x,0), m)$. A natural way to approach this task is to examine more closely the structure of $\mathcal{C}$ near $(\lambda_1^+(d(x,0), m), 0)$, i.e. make a local bifurcation analysis around the bifurcation point in the parlance of bifurcation theory. For then, if $\mathcal{C}$ 'bends to the left in parameter space' at $(\lambda_1^+(d(x,0), m), 0)$, it must be the case that $\underline{\lambda} < \lambda_1^+(d(x,0), m)$. The proper tool for the job is the well-known constructive bifurcation theorem of Crandall and Rabinowitz [5], which is applicable under the hypotheses of assumptions 2.1 and guarantees the following.

THEOREM 2.7. *Assume that assumptions 2.1 hold. Let $\phi_1$ denote the unique positive solution of (1.5) satisfying*

$$\int_\Omega \phi_1^2 = 1.$$

*Then there is an interval $(-s_0, s_0)$ about 0 in $\mathbb{R}$ and two twice continuously differentiable functions $\varphi : (-s_0, s_0) \to C_0^{2+\alpha}(\bar{\Omega})$ and $\mu : (-s_0, s_0) \to \mathbb{R}$ such that*

(i) $\varphi(0) = 0 = \varphi'(0)$;

(ii) $\mu(0) = 0$;

(iii) $(\lambda_1^+(d(x,0), m) + \mu(s), s\phi_1 + \varphi(s))$ *give all non-trivial solutions to* $F(\lambda, u) = 0$ *in a neighbourhood of* $(\lambda_1^+(d(x,0,m), 0)$ *in* $\mathbb{R} \times C_0^{2+\alpha}(\bar{\Omega})$.

REMARK 2.8. The choice of $\phi_1$ and condition (i) of theorem 2.7 guarantee that near $(\lambda_1^+(d(x,0), m), 0)$, $\mathcal{C}$ is described by (iii) for $s \in [0, s_0)$.

REMARK 2.9. $\mathcal{C}$ 'bends to the left in parameter space' if $\mu'(0) < 0$.

We next calculate $\mu'(0)$.

LEMMA 2.10. *$\mu'(0)$ satisfies the equation*

$$0 = \int_\Omega d_u(x,0)\phi_1|\nabla\phi_1|^2 - \mu'(0)\int_\Omega m(x)\phi_1^2 + \lambda_1^+(d(x,0), m)\int_\Omega c\phi_1^3. \tag{2.3}$$

*Proof.* Substitute $(\lambda_1^+(d(x,0), m) + \mu(s), s\phi_1 + \varphi(s))$ into $F(\lambda, u) = 0$, differentiate twice with respect to $s$ and evaluate at $s = 0$. Then $\varphi''(0) \in C_0^{2+\alpha}(\bar{\Omega})$ satisfies

$$\begin{aligned} &-\nabla\cdot(d(x,0)\nabla\varphi''(0)) - \lambda_1^+(d(x,0), m(x))m(x)\varphi''(0) \\ &\qquad = 2(\nabla\cdot(d_u(x,0)\phi_1\nabla\phi_1) + \mu'(0)m(x)\phi_1 - \lambda_1 c\phi_1^2). \end{aligned} \tag{2.4}$$

Multiplying (2.4) by $\phi_1$, integrating over $\Omega$ and employing Green's second identity yields

$$0 = -\int_\Omega \phi_1\nabla\cdot(d_u(x,0)\phi_1\nabla\phi_1) - \mu'(0)\int_\Omega m(x)\phi_1^2 + \lambda_1^+(d(x,0), m)\int_\Omega c\phi_1^3. \tag{2.5}$$

By applying the divergence theorem to the first term on the right-hand side of (2.5), we obtain (2.3). □

We now consider (2.3). It follows from (1.5) that

$$\int_\Omega d(x,0)|\nabla\phi_1|^2 = \lambda_1^+(d(x,0), m)\int_\Omega m(x)\phi_1^2,$$

so that

$$\int_\Omega m(x)\phi_1^2 > 0$$

and

$$\mu'(0) = \frac{\int_\Omega d_u(x,0)\phi_1|\nabla\phi_1|^2 + \lambda_1^+(d(x,0), m)\int_\Omega c\phi_1^3}{\int_\Omega m(x)\phi_1^2}. \tag{2.6}$$

Consequently, $\mu'(0) < 0$ if and only if the numerator on the right-hand side of (2.6) is negative. We hypothesize in assumption 2.1 (v) that $d_u(x,0) < 0$ on $\bar{\Omega}$. There are several ways in which one can refine this hypothesis to obtain a sufficient condition guaranteeing that $\mu'(0) < 0$. We illustrate two of them. If

$$d_u(x,0) < d_1 d(x,0), \quad \text{where } d_1 < 0, \tag{2.7}$$

then

$$\mu'(0) \leqslant \frac{d_1 \int_\Omega d(x,0)\phi_1|\nabla\phi_1|^2 + \lambda_1^+(d(x,0),m)\int_\Omega c\phi_1^3}{\int_\Omega m(x)\phi_1^2}. \tag{2.8}$$

Consider $\int_\Omega d(x,0)\phi_1|\nabla\phi_1|^2$. By (1.5), we have

$$-\nabla\cdot(d(x,0)\nabla\phi_1) = \lambda_1^+(d(x,0),m)m(x)\phi_1$$

on $\Omega$. Multiplying by $\phi_1^2$ on both sides, integrating over $\Omega$ and employing the divergence theorem yields

$$\int_\Omega d(x,0)\nabla(\phi_1^2)\cdot\nabla\phi_1 = \lambda_1^+(d(x,0),m)\int_\Omega m(x)\phi_1^3. \tag{2.9}$$

Since $\nabla(\phi_1^2) = 2\phi_1\nabla\phi_1$, it follows from (2.9) that

$$\int_\Omega d(x,0)\phi_1|\nabla\phi_1|^2 = \tfrac{1}{2}\lambda_1^+(d(x,0),m)\int_\Omega m(x)\phi_1^3. \tag{2.10}$$

We have from (2.8) and (2.10) that $\mu'(0) < 0$ if

$$\int_\Omega (d_1 m(x) + 2c)\phi_1^3 < 0. \tag{2.11}$$

If now $m(x) > m_0 > 0$ on $\Omega$, equation (2.11) obtains if

$$d_1 m_0 + 2c < 0. \tag{2.12}$$

Note that if $d_u(x,0) = d_1 d(x,0)$ and $m(x) = m_0$,

$$\mu'(0) = \lambda_1^+(d(x,0),m)\left(\tfrac{1}{2}d_1 + \frac{c}{m_0}\right)\int_\Omega \phi_1^3,$$

which is negative if and only (2.12) holds, making (2.12) a sharp condition in this case.

Another way to refine assumption 2.1 (v) is simply to assume

$$d_u(x,0) \leqslant d_0 < 0. \tag{2.13}$$

If (2.13) holds, then

$$\mu'(0) \leqslant \frac{d_0 \int_\Omega \phi_1|\nabla\phi_1|^2 + \lambda_1^+(d(x,0),m)\int_\Omega c\phi_1^3}{\int_\Omega m(x)\phi_1^2}. \tag{2.14}$$

Observe that

$$\begin{aligned}\int_\Omega \phi_1|\nabla\phi_1|^2 &= \int_\Omega \phi_1^{1/2}\nabla\phi_1\cdot\phi_1^{1/2}\nabla\phi_1\\ &= \int_\Omega |\tfrac{2}{3}\nabla\phi_1^{3/2}|^2\\ &= \frac{4}{9}\int_\Omega |\nabla\phi_1^{3/2}|^2\\ &\geqslant \tfrac{4}{9}\lambda_0(\Omega)\int_\Omega (\phi_1^{3/2})^2\\ &= \tfrac{4}{9}\lambda_0(\Omega)\int_\Omega \phi_1^3,\end{aligned}$$

where $\lambda_0(\Omega) > 0$ is the principal eigenvalue of the Laplace operator on $\Omega$ subject to homogeneous Dirichlet boundary conditions. From (2.14) and the inequality

$$\int_\Omega \phi_1|\nabla\phi_1|^2 \geqslant \tfrac{4}{9}\lambda_0(\Omega)\int_\Omega \phi_1^3, \tag{2.15}$$

we have that $\mu'(0) < 0$, provided

$$\tfrac{4}{9}d_0\lambda_0(\Omega) + \lambda_1^+(d(x,0),m)c < 0. \tag{2.16}$$

Summarizing, we have the following result.

THEOREM 2.11. *$\mu'(0) < 0$ if either*

(i) *equations (2.7) and (2.11) hold; or*

(ii) *equations (2.13) and (2.16) hold.*

As we have noted, problem (1.3) admits positive equilibria for $\lambda$ below the critical threshold $\lambda_1^+(d(x,0),m)$, provided $\mu'(0) < 0$. In fact, in this case, the connectivity of $\mathcal{C}$, the existence of a positive equilibrium for (1.3) when $\lambda = \lambda_1^+(d(x,0),m)$ and the representation of $\mathcal{C}$ near $(\lambda_1^+(d(x,0),m),0)$ in theorem 2.7 collectively imply that there is an interval $(\lambda^*,\lambda_1^+(d(x,0),m))$ in $\lambda$ such that if $\lambda \in (\lambda^*,\lambda_1^+(d(x,0),m))$, problem (1.3) admits at least two positive equilibria.

In the last portion of our analysis of the positive equilibria of (1.3), we focus on the asymptotics of (1.3) for $\lambda$ close to but below $\lambda_1^+(d(x,0),m)$. We know from lemma 1.3 that the 0 equilibrium is stable for such $\lambda$. To proceed further, we formulate some eigenvalue problems. Notice that

$$F_u(\lambda,u)\phi = \nabla\cdot(d(x,u)\nabla\phi) + \nabla\cdot(d_u(x,u)\phi\nabla u) + \lambda[m(x)\phi - 2cu\phi] \tag{2.17}$$

for $\phi \in C_0^{2+\alpha}(\bar{\Omega})$. When $u = 0$, equation (2.17) reduces to

$$F_u(\lambda,0)\phi = \nabla\cdot(d(x,0)\nabla\phi) + \lambda m(x)\phi. \tag{2.18}$$

Let $\sigma(\lambda,u)$ denote the principal eigenvalue for (2.17), i.e. $\sigma = \sigma(\lambda,u)$ is the unique real number for which

$$\left.\begin{aligned} F_u(\lambda,u)\phi &= \sigma\phi \quad &&\text{in } \Omega,\\ \phi &= 0 &&\text{on } \partial\Omega\end{aligned}\right\} \tag{2.19}$$

admits an eigenfunction $\phi$ with $\phi > 0$ in $\Omega$. Lemma 1.1 shows that

$$\sigma(\lambda_1^+(d(x,0),m),0) = 0.$$

If $\sigma(\lambda, u) > 0$ and $\phi > 0$ is a corresponding eigenfunction in (2.19), [4] shows that for all sufficiently small $\varepsilon > 0$,

$$w_\varepsilon(\lambda, u) = u + \varepsilon\phi - \varepsilon^2 \frac{d_u(x,u)}{2d(x,u)}\phi^2$$

is a lower solution to $F(\lambda, u) = 0$ viewed as an elliptic differential equation, and, consequently, that if $\tilde{u}_\varepsilon(x,t)$ is the solution to (1.3) with $\tilde{u}_\varepsilon(x,0) = w_\varepsilon(\lambda,u)(x)$, then $\tilde{u}_\varepsilon(x,t)$ is monotonically increasing in $t$ with $\lim_{t\to\infty} \tilde{u}_\varepsilon(x,t) = \bar{u}(x)$, where $\bar{u}(x)$ is a positive equilibrium to (1.3) such that $\bar{u}(x) > u(x)$ on $\Omega$ (see also [1]). Since (1.3) is order preserving, if $w$ is a solution to (1.3) with $w(x,0) \geqslant w_\varepsilon(\lambda,u)(x)$, then $w(x,t) \geqslant \tilde{u}_\varepsilon(x,t)$ for all $t > 0$. Hence, for any $\delta \in (0,1)$, $w(x,t) > (1-\delta)\bar{u}(x)$ for all $x \in \Omega$ and all sufficiently large $t$. Consequently, if there is a positive equilibrium $u$ for (1.3) for some $\lambda < \lambda_1^+(d(x,0),m)$ with the property that $\sigma(\lambda,u) > 0$, the asymptotics for (1.3) for that $\lambda$ are dramatically different from the case described in theorem 1.2. In the next section we analyse in detail the ecological ramifications of such a phenomenon.

All that remains to be seen is whether we can find parameter-equilibrium pairs $(\lambda, u)$ with $\lambda < \lambda_1^+(d(x,0),m)$ and $\sigma(\lambda,u) > 0$. To this end, for $s \in [0, s_0)$, let

$$\sigma(s) = \sigma(\lambda_1^+(d(x,0),m) + \mu(s), s\phi_1 + \varphi(s)), \tag{2.20}$$

where

$$(\lambda_1^+(d(x,0),m) + \mu(s), s\phi_1 + \varphi(s))$$

is the parametrization of $\mathcal{C}$ near $(\lambda_1^+(d(x,0),m),0)$ given in theorem 2.7. In [6], the sign of $\sigma(s)$ for $s$ near 0 is related to the rate of change of the $\lambda$ component of $\mathcal{C}$ with respect to $s$ ($\mathrm{d}\mu/\mathrm{d}s(s)$) and the rate of change of $\sigma(\lambda,0)$ with respect to $\lambda$ at

$$\lambda = \lambda_1^+(d(x,0),m)\left(\frac{\partial\sigma}{\partial\lambda}(\lambda_1^+(d(x,0),m),0)\right).$$

Specifically,

$$\operatorname{sgn}(\sigma(s)) = \operatorname{sgn}\left(-s\frac{\mathrm{d}\mu}{\mathrm{d}s}(s)\frac{\partial\sigma}{\partial\lambda}(\lambda_1^+(d(x,0),m),0)\right). \tag{2.21}$$

If $\mathrm{d}\mu/\mathrm{d}s(0) < 0$ (as may be guaranteed by theorem 2.11), $\mathrm{d}\mu/\mathrm{d}s(s) < 0$ for $s > 0$ and sufficiently small. Consequently, it follows from (2.21) that $\sigma(s) > 0$ for all $s > 0$ and sufficiently small, provided that we find that

$$\frac{\partial\sigma}{\partial\lambda}(\lambda_1^+(d(x,0),m),0) > 0.$$

Consequently, we conclude this section with a proof of this fact.

PROPOSITION 2.12. *Let $\sigma = \sigma(\lambda,0)$ denote the unique real value, so that*

$$\begin{aligned} F_u(\lambda,0)\phi &= \sigma\phi \quad \text{in } \Omega, \\ \phi &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

*admits an eigenfunction $\phi > 0$. Then*

$$\frac{\partial \sigma}{\partial \lambda}(\lambda_1^+(d(x,0),m),0) > 0.$$

*Proof.* Suppose for all $\lambda$ that $\phi$ is normalized by requiring

$$\int_\Omega \phi^2 = 1.$$

Then $\phi_\lambda = (\partial\phi/\partial\lambda)(\lambda,0)$ and $\sigma_\lambda = \partial\sigma/\partial\lambda$ exist and we may calculate

$$\frac{\partial \sigma}{\partial \lambda}(\lambda_1^+(d(x,0),m),0)$$

from $F_u(\lambda,0)\phi = 0$. Differentiating $F_u(\lambda,0)\phi = 0$ with respect to $\lambda$ yields

$$\nabla \cdot (d(x,0)\nabla\phi_\lambda) + m(x)\phi + \lambda m(x)\phi_\lambda = \sigma_\lambda\phi + \sigma\phi_\lambda. \tag{2.22}$$

Multiplying (2.22) by $\phi$, integrating and applying the divergence theorem yields

$$\int_\Omega \phi_\lambda(\nabla \cdot d(x,0)\nabla\phi + \lambda m(x)\phi) + \int_\Omega m(x)\phi^2 = \sigma_\lambda + \sigma\int_\Omega \phi\phi_\lambda, \tag{2.23}$$

as

$$\int_\Omega \phi^2 = 1.$$

Since $F_u(\lambda,0)\phi = \sigma\phi = \sigma(\lambda,0)\phi$, equation (2.23) simplifies to

$$\sigma_\lambda = \int_\Omega m(x)\phi^2.$$

Hence

$$\frac{\partial \sigma}{\partial \lambda}(\lambda_1^+(d(x,0),m),0) = \int_\Omega m(x)\phi_1^2,$$

which we observed to be positive following the proof of lemma 2.10. □

Summarizing, we have the following result.

THEOREM 2.13. *Suppose assumptions 2.1 hold, $(\lambda_1^+(d(x,0),m)+\mu(s), s\phi_1+\varphi(s))$ is as in theorem 2.7 (iii), and that $\mu'(0) < 0$. Then if $\sigma(s)$ is as in (2.20), $\sigma(s) > 0$ for $s > 0$ and sufficiently small. Consequently, there is an interval $(\lambda^{**}, \lambda_1^+(d(x,0),m))$ in $\mathbb{R}$ such that, for $\lambda \in (\lambda^{**}, \lambda_1^+(d(x,0),m))$, problem (1.3) admits a minimal positive equilibrium $u = u(\lambda)$. Moreover, for such $\lambda$, there is an equilibrium $\bar{u}$ of (1.3) with $\bar{u} > u$ on $\Omega$, so that, for any $\delta \in (0,1)$ and any solution $w$ of (1.3) with $w(x,0)$ strictly larger than $u(x)$ on $\Omega$, there is a $\bar{t}$ such that that $w(x,t) \geqslant (1-\delta)\bar{u}(x)$ on $\Omega$ for $t \geqslant \bar{t}$.*

REMARK 2.14. The notion '$w(x,0)$ strictly larger than $u(x)$ on $\Omega$' means that $w(x,0)$ exceeds $u(x)$ on $\Omega$ and that the outer normal derivatives $(\partial w/\partial\eta)(x,0)$ and $(\partial u/\partial\eta)(x)$ on $\partial\Omega$ satisfy

$$\frac{\partial w}{\partial \eta}(x,0) < \frac{\partial u}{\partial \eta}(x) < 0.$$

For such a $w$, there is a $\varepsilon > 0$ such that $w(x,0) \geqslant w_\varepsilon(\lambda,u)(x)$, and it is then evident that the last statement in theorem 2.13 is correct.

## 3. Discussion

### 3.1. A simple example

To explicate the results of § 2, let us consider the model

$$\left.\begin{aligned} \frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(d(u)\frac{\partial u}{\partial x}\right) + r\left(1 - \frac{u}{K}\right)u \quad \text{on } (0,\ell)\times(0,\infty), \\ u(0,t) = u(\ell,t) = 0 \quad \text{for } t > 0. \end{aligned}\right\} \tag{3.1}$$

By rescaling space via $\xi = x/\ell$ as in § 1, model (3.1) becomes

$$\left.\begin{aligned} \frac{\partial u}{\partial t} = \frac{1}{\ell^2}\frac{\partial}{\partial \xi}\left(d(u)\frac{\partial u}{\partial \xi}\right) + r\left(1 - \frac{u}{K}\right)u \quad \text{on } (0,1)\times(0,\infty), \\ u(0,t) = u(1,t) = 0 \quad \text{for } t > 0, \end{aligned}\right\} \tag{3.2}$$

where $u$ should now be interpreted as $u(\xi,t)$. The equilibrium problem can be written as

$$\left.\begin{aligned} 0 = \frac{\partial}{\partial \xi}\left(d(u)\frac{\partial u}{\partial \xi}\right) + \ell^2\left(ru - \frac{r}{K}u^2\right) \quad \text{in } (0,1), \\ u(0) = u(1) = 0. \end{aligned}\right\} \tag{3.3}$$

We can now identify the parameters as $\lambda = \ell^2$, $m = r$ and $c = r/K$. Also, since $d(u)$ does not involve $x$, we see that $d(0)$ and $d_u(0)$ are constants. We have $\lambda_1^+(d(0), r) = d(0)\pi^2/r$ and we may choose $\phi_1(\xi) = \sin(\pi\xi)$. Thus the condition for invasibility of the habitat, i.e. the condition for the equilibrium $u \equiv 0$ to be unstable, is

$$\ell^2 > \frac{d(0)\pi^2}{r}. \tag{3.4}$$

This is the standard formulation for the minimum patch size that will sustain a population in the case of diffusion without density dependence (see [3] and the references therein).If we allow density dependence, then we may compute $\mu'(0)$ via (2.6) to obtain

$$\mu'(0) = \frac{4\pi}{3r}\left[d_u(0) + \frac{2d(0)}{K}\right], \tag{3.5}$$

so that $\mu'(0)$ satisfies

$$\mu'(0) < 0 \quad \text{if and only if } \frac{d_u(0)}{d(0)} < -\frac{2}{K}. \tag{3.6}$$

Finally, if $d_0 = \inf_{u>0} d(u)$, then the argument used in corollary 3.2 of [3] shows that no positive equilibrium can exist in (3.3) and hence for (3.1) unless

$$\ell^2 > \lambda_1^+(d_0, r) = \frac{d_0\pi^2}{r}. \tag{3.7}$$

The analyses of [3] and the previous section now imply that for $\ell > (\sqrt{d(0)/r})\pi$, the equilibrium $u = 0$ of (3.1) is unstable, so that the habitat is invasible, i.e. populations at low densities will increase. For such values of $\ell$, the model predicts unconditional persistence. If $d_u(u) \geqslant 0$, then for $\ell \leqslant \pi\sqrt{d(0)/r}$, all solutions to (3.1) will

approach zero as $t \to \infty$, so that the minimum patch size for invasibility is the same as the minimum patch size that can sustain a population [3]. However, if $d_u(0)/d(0) < -2/K$, then there will be a value $\ell_0 \in [\sqrt{d_0/r\pi}, \sqrt{d(0)/r\pi})$ such that for $\ell_0 \leqslant \ell < \sqrt{d(0)/r\pi}$ the equilibrium $u = 0$ will be stable, so small populations will die out, but there will be at least two positive equilibria. For values of $\ell$ close to, but slightly less than, $\sqrt{d(0)/r\pi}$, the smallest positive equilibrium will be unstable in the sense that any solution of (3.1) that is initially larger than the minimal positive equilibrium will remain larger for all time and will be bounded below by a solution that will increase toward the second smallest positive equilibrium. Thus, in that case, the model predicts a type of conditional persistence analogous to that found in models with an Allee effect built into the terms describing local population dynamics. Also, in this situation, the model displays a 'hysteresis' effect in the sense that if there is a large population inhabiting a large patch and $\ell$ is reduced, the population may remain relatively large even as $\ell$ is decreased below $\sqrt{d(0)/r\pi}$, so that the patch is no longer invasible, but then experience a sudden collapse if $\ell$ is decreased further so that $\ell < \ell_0$. The closer $\ell_0$ is to $\sqrt{d(0)/r\pi}$, the more sudden will be the onset of such an irrevocable collapse.

## 4. General conclusions

### 4.1. Conditional persistence via aggregation

Non-spatial logistic models and logistic models augmented by dispersal via passive diffusion can only predict *unconditional* persistence or extinction; that is, they either predict persistence for any population with a positive initial density or extinction for any population [3]. If a logistic model is augmented by dispersal via a density-dependent diffusion process, where individuals disperse more slowly in the presence of conspecifics at low densities, it may predict *conditional* persistence for some parameter ranges. In other words, the model may predict extinction for populations with low initial densities but persistence for populations with high initial densities. This sort of behaviour is typical of population models where an Allee effect is built into the description of the population dynamics, but in our models the population dynamics are assumed to be logistic, so the effect is induced only because of the aggregative density-dependent dispersal. A biological interpretation of the mechanism is that at low population densities individuals disperse rapidly and are likely to encounter the hostile exterior of their habitat, while at slightly higher densities they disperse less rapidly and thus experience reduced mortality due to dispersal into hostile environments. If that effect is sufficiently strong relative to the logistic effect of intraspecific competition, then the net population growth rate may be greater at moderately high densities than at low densities. If the net population growth rate is positive at moderately high densities and negative at low densities, then the model predicts conditional persistence.

Both logistic models with passive diffusion and logistic models with density-dependent aggregative diffusion predict a minimum size for a patch with a lethal boundary to be able to sustain a population. However, density-dependent diffusion can change the minimal patch size and the way in which a stable population equilibrium behaves as patch size decreases. In the case of passive diffusion, the stable equilibrium density decreases smoothly toward zero as the patch size decreases

toward the minimum size that allows population growth at low densities. In the case of aggregative density-dependent dispersal, there can be stable equilibria with relatively large population densities, even though the patch size is decreased below the minimum size that would allow population growth at low densities. However, if patch size is decreased further, then the population may collapse suddenly to zero. Furthermore, if the population is at a stable equilibrium in a patch that is too small to allow population growth at low densities, and the population is reduced by a catastrophic event such as an epidemic or natural disaster, it may not be able to recover.

The mechanism by which an aggregating population may be able to maintain a positive equilibrium density on a patch that is too small to allow growth at low densities is the formation of aggregations that are far enough from the lethal patch boundary to avoid its deleterious effects. Such aggregations can only form if the density is sufficiently high. At low densities, the population will disperse more rapidly and thus encounter the lethal boundary. However, if patch size decreases further, aggregation will no longer insulate the population from the effects of the boundary, and a collapse may ensue.

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